BIOCHEMISTRY AND FUNCTION OF CRUSTACEAN NEUROHORMONES

Triggered by various environmental stimuli, the nervous system produces and releases several peptides which enable an organism to handle specific situations. The regulatory potencies of the peptides so far postulated include cardiac control, locomotion, feeding behaviour, migration of chromatophores and retinal pigment, moult suppression/acceleration, the development of testis, oocytes and vitellogenin, limb regeneration, blood glucose adjustment, endogenous rhythmicity, lipid, carbohydrate and protein metabolism, osmo- and hydromineral and respiratory regulation, RNA/DNA synthesis, mitochondrial respiration and carotinoid metabolism: almost every aspect of crustacean life. The number of postulated factors is large (Kleinholz, 1985; Webster and Keller, 1988), the number of isolated neurohormonal peptides, however, is small and our knowledge of their physiological functions is still limited. Several factors are based on inadequate evidence or are still under discussion e.g. the neurodepressing hormone (Cooke and Sullivan, 1982). In terms of the amino acid composition, the moult-inhibiting hormone (MIH) from *Carcinus maenas*, the crustacean hyperglycemic hormones (CHH) from *Orconectes limosus*, *Porcellio dilatatus* and *Procambarus bouvieri* and the neurodepressing hormone from various species have been characterized. The primary sequence is reported for two FMRF-like peptides (FLI), a member of the pigment concentrating hormone family, from two pigment dispersing hormones, from cardioactive peptides and from the CHH of *Carcinus maenas* (Kegel *et al.*, 1989). For this 8524 Da neuropeptide the complete coding sequence for the pre-pro CHH has been obtained recently from a DNA-library (Weidemann *et al.*, 1989). MIH and the gonad (vitellogenin) inhibiting hormone (GIH/VIH) apparently belong to the CHH neuropeptide family, judging by the comparison of amino acid sequences, which have been analysed to approximately 80%. Recent observations are consistent with the hypothesis that the spectrum of functions of these identified neurohormones might be broader than their names suggest. The red pigment concentrating hormone (RPCH), for example, affects not only the erythrophores but also the pyloric rhythms by alternating the membrane potential in the lateral pyloric and pyloric dilator motor neurons. Therefore, RPCH (or a very similar molecule) is thought to release a modulator from the somatogastric ganglion. A similar modulation of proctolin on the pyloric network has been reported. In addition to glucose CHH affects trehalose and maltose blood concentrations and releases amylase from the midgut gland in crayfish. The distribution of the crustacean-cardioactive peptide (CCAP) in the central nervous system suggests that CCAP might be a novel neurotransmitter with multiple functions, e.g. modulation of the motility of isolated hindguts. In addition to these neuropeptides, which are derived from neurohemal sources such as the sinus gland or pericardial organ, numerous, mainly vertebrate-type peptides, have been described in crustacean neuronal tissue using immunocytochemical methods. The stained epitope does not necessarily prove the identity of the original antigen, either functionally or biochemically. Some of these X-like peptides with limited or no relation to vertebrate hormones, such as cholecystokinin/gastrin-like or calcitonin-like peptides have been isolated or sequenced. The physiological functions of these peptides are mostly unknown or the subject of speculation. Opioid- and FMRFamide-like peptides have been demonstrated by HPLC, RIA and immunocytochemistry in decapod crustaceans (Jaros, 1990). The FMRFamide-like peptides (FLI3,4), isolated from *Homarus*, seem to be involved in the modulation of cardiac neuromuscular junctions (Trimmer *et al.*, 1987). The CHH release-inhibiting effect of leu-enkephalin, blocked by naloxone, was shown by Jaros *et al.* (1985). Met-enkephalin has been shown to stimulate the release of chromatophorotropic hormones and other evidence exists for the involvement of an opioid regulation of locomotor activity in *Gecarcinus lateralis*. These different results demonstrate the broad spectrum of opioid effects on crustacean physiology. An exciting future field of study for the endocrinologist is the growing body of information regarding a possible neurohormonal-immunological axis even in invertebrates. Pilot studies reveal an implication of opioids on hemocyte aggregation.

Acknowledgement

The work is supported by the Deutsche Forschungsgemeinschaft (Ja 397/2-1).

Literature Cited

Cooke, I.M. and Sullivan, R.E. 1982. Hormones and Neurosecretion. 205–290. In H.L. Atwood and D.C. Sandeman (eds) 'The biology of Crustacea', Vol. 3. (Academic Press: New York).

Jaros, P.P., Dircksen, H. and Keller, R. 1985. Occurrence of immunoreactive enkephalins in a neurohaemal organ and other nervous structures in the eyestalk of the shore crab, *Carcinus maenas* L. (Crustacea, Decapoda). Cell and Tissue Research **241**: 111–117.

Jaros, P.P. 1990. Enkephalins, biologically active neuropeptides in invertebrates, with special references to crustaceans. 471–482. In K. Wiese, W.D. Krenz, J. Tautz, H. Reichert and B. Mulloney (eds) 'Frontiers in crustacean neurobiology'. (Birkhauser: Basel).

Kegel, G., Reichwein, B., Weese, S., Gaus, G., Peter-Katalinic, J. and Keller, R. 1989. Amino acid sequence of the crustacean hyperglycemic hormone (CHH) from the shore crab, *Carcinus maenas*. FEBS Letters **255**: 10–14.

Kleinholz, L.H. 1985. Biochemistry of Crustacean Hormones. Pp. 463–522. In D.E. Bliss and L.H. Mantel (eds) 'The biology of Crustaceans', Vol. 9. (Academic Press: New York)

Trimmer, B.A., Kobierski, L.A. and Kravitz, E.A. 1987. Purification and characterization of FMRFamide-like immunoreactive substances from the lobster nervous system: isolation and sequence analysis of two closely related peptides. Journal of Comparative Neurology **266**: 16–26.

Webster, S.G. and Keller, R. 1988. Physiology and biochemistry of crustacean neurohormonal peptides. 173–196. In M.C. Thorndyke and G.J. Goldsworthy (eds) 'Neuropeptides in Invertebrates'. (Cambridge University Press: Cambridge).

Weidemann, W., Gromoll, J. and Keller, R. 1989. Cloning and sequence analysis of cDNA for precursor of a crustacean hyperglycemic hormone. FEBS Letters **257**: 31–34.

Peter P. Jaros, University of Oldenburg, Department of Animal Physiology, Germany.